## STUDIES IN NEOTROPICAL LEPTOCERIDAE (TRICHOPTERA), VI: IMMATURE STAGES OF *HUDSONEMA FLAMINII* (NAVÁS) AND THE EVOLUTION AND HISTORICAL BIOGEOGRAPHY OF HUDSONEMINI (TRIPLECTIDINAE)

RALPH W. HOLZENTHAL

Department of Entomology, Clemson University, Clemson, South Carolina 29634-0365.

*Abstract.* — The larval and pupal stages of the Chilean species *Hudsonema flaminii* (Navás) (Triplectidinae: Hudsonemini) are described and illustrated for the first time. The larva is characterized by the presence of secondary setae on the lateral sclerite of each anal proleg and by the brown-spotted head and thorax. Adult genitalia and wing venation of both sexes are redescribed and illustrated. A key to adults of the Neotropical triplectidine genera is provided. *Triplectides fazi* Navás is a synonym of *H. flaminii*, **New Synonym.** The evolution and historical biogeography of the Hudsonemini are discussed. *Hudsonema* is most closely related to the Australian genus *Condocerus*; its distribution conforms to a New Zealand-South American trans-Antarctic biogeographical track.

The long-horned caddisfly genus *Hudsonema* Mosely contains three described species: *H. aliena* (Mac Lachlan), *H. amabilis* (Mac Lachlan), both from New Zealand, and *H. flaminii* (Navás), an austral South American endemic. The distributions of these species conform to a trans-Antarctic, Australasian-Neotropical biogeographical track. Within the Trichoptera, exclusively trans-Antarctic distributions are found in the families Helicophidae, Kokiriidae, Philorheithridae, and Tasimiidae, and, within the Leptoceridae, in the genera *Hudsonema, Notalina,* and *Triplectides* (Holzenthal, 1986). *Hudsonema,* however, is the only leptocerid genus that exhibits an exclusively New Zealand-South American trans-Antarctic track, considered by Craw (1979, 1982) to be distinct from the Australian-South American trans-Antarctic track displayed by *Notalina* and *Triplectides.*

Mosely (1936) erected the genus *Hudsonema,* designated the New Zealand species *Tetracentron amabile* Mac Lachlan as the type species and transferred two South American species, *Triplectides discolor* Navás and *Triplectides flaminii* Navás, to his new genus. Later, Mosely and Kimmins (1953) transferred an additional New Zealand species, *Leptocerus alienus* Mac Lachlan to *Hudsonema* and described two new species, *H. maculata* and *H. sparsa,* both from Australia and Tasmania. Neboiss (1977) recognized that the two Australian species, *H. maculata* and *H. sparsa,* differed considerably from the type species in both genitalic and venational characters and transferred them to a new genus, *Notoperata* Neboiss. Flint (1974) synonymized *H. discolor* (Navás) with *H. flaminii* (Navás). A specimen from the NMNH bearing the labels "CHILE: Valpo. Est.

Marga-Marga, nr. Perales 9 Mar. 1968 Flint & Pena" and "COMP. w. TYPE Triplectides fazi Nav. by Flint '76" is in fact a female of *Hudsonema flaminii*. I accept Flint's determination and consider *Triplectides fazi* Navás, 1932, to be a junior synonym of *Hudsonema flaminii* (Navás), 1926, **New Synonym**. The adult male and female genitalia and wing venation of *Hudsonema flaminii* have been described and illustrated previously by Mosely (1936, fig. 63–66) and Schmid (1950, fig. 105–110). Cowley (1978) described the larvae of the two New Zealand species and briefly discussed their biology. In the present paper, the larval and pupal stages of *Hudsonema flaminii* are described and figured for the first time. Redescriptions and illustrations of the adults of both sexes are also provided. A key to adults of the Neotropical triplectidine genera is included. Finally, the evolution and historical biogeography of the Hudsonemini are discussed.

Terminology for wing venation and female genitalia follows the review by Schmid (1980) and that for male genitalia, those of Nielsen (1957), Morse (1975), and Schmid (1980). Terminology for larval and pupal morphology follows the reviews by Wiggins (1977, 1984). Larval setal nomenclature and homology follows that of Williams and Wiggins (1981). All material examined is from the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH). Distribution data are indicated by country and province. Complete collection records for only those specimens examined in preparing larval and pupal descriptions and illustrations are provided below.

### Hudsonema flaminii (Navás)
Figs. 1–5

*Triplectides flaminii* Navás 1926: 335, fig. 49 a–b; Navás 1929: 24; Navás 1930: 363.

*Triplectides discolor* Navás 1932a: 83, fig. 13; Navás 1933: 234.

*Hudsonema flaminii*, Mosely 1936: 111, fig. 63–68; Schmid 1950: 361, fig. 105–108; Flint 1967: 60; Flint 1974: 90, distribution.

*Hudsonema discolor*, Mosely 1936: 114; Schmid 1950: 362. fig. 109–110; Flint 1974: 84, synonym of *H. flaminii*.

*Triplectides fazi* Navás 1932b: 84, fig. 73; Mosely 1936: 126. New Synonym.

*Adult:* Tibial spur formula 2, 2, 4. Forewing (Fig. 5A) with forks I and V present in male; I, III, and V present in female; fork I distinctly petiolate; discal and thyridial cells subequal in length. Hindwing (Fig. 5B) with forks I, III, and V present in both sexes; forks I and V deep; discal cell present. General body color brown, with scattered white hairs on head and thorax; longitudinal white bands of hairs on forewing, especially in male (Mosely 1936, fig. 63); female forewing sometimes completely brown. Length of forewing 13–15 mm male, 9–11 mm female.

*Male:* Abdominal segment IX annular, anterior margin sinuate; tergum IX produced posteriorly, rounded in dorsal view, and forming dorsal shelf over bases of preanal appendages; lateral portions of IX produced posteriorly as setose, finger-like to triangular projections (Figs. 3A, 3B). Segment X with pair of long, slender, dorsomesal processes and pair of long, thin, gradually upturned, ventrolateral processes; ventrolateral processes each terminating in single seta (Figs. 3A, 3B). Preanal appendages broad, flat, heavily setose; apices acute (Fig. 3B). Inferior
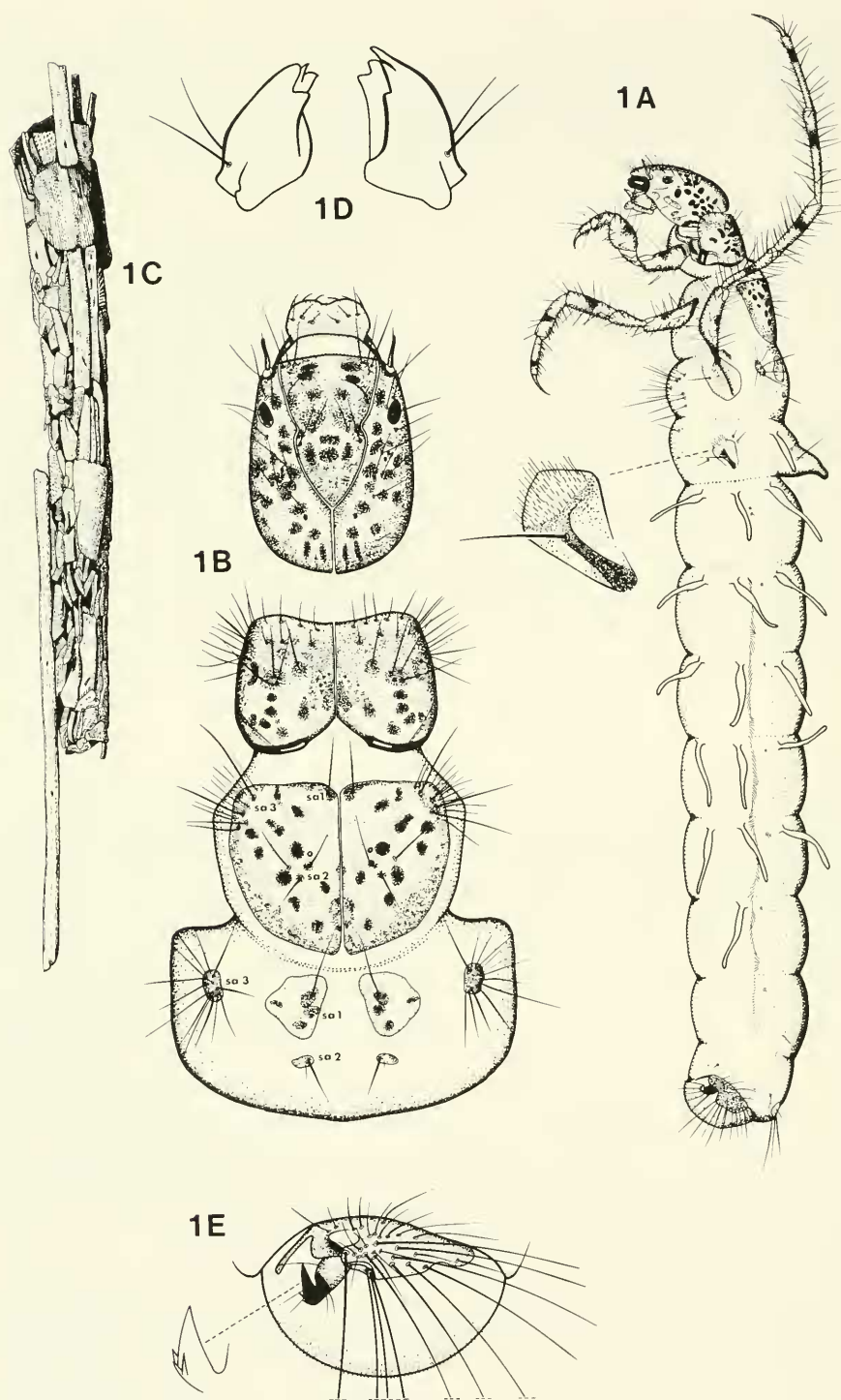
Fig. 1. *Hudsonema flaminii* (Navás), larva and case. A, Larva, lateral, lateral hump sclerite enlarged. B, Head and thorax, dorsal. C, Case, lateral. D, Mandibles, ventral. E, Anal proleg and abdominal segment X, lateral, anal claw enlarged.

appendages short and stout, more or less quadrate in general outline in lateral view (Fig. 3A); each with 4 terminal processes: dorsolateral (*dl*) and ventrolateral (*vl*) processes short, thumb-shaped in ventral view (Fig. 3C); ventromesal process (*vm*) short, slender, inconspicuous; dorsomesal process (*dm*) long, somewhat sinuate, sharply pointed; ventrobasal angle broadly rounded in lateral view, subrectilinear and next to the meson in ventral view; inferior appendages broadly connected basally (Fig. 3C). Phallic apparatus simple, short and slender; phallotremal sclerite with dorsal projections (Fig. 3D).

*Female:* Sternum IX distinctive; developed into broad, slightly concave, sclerotized plate; posterior portion shaped somewhat like head of a planarian (Fig. 4B). Valves long, flat, each bordered ventrally with short setae; appendages of segment X short, heavily setose (Figs. 4A, 4B).

*Egg:* Unknown.

*Larva:* Head (Figs. 1A, 1B, 2A): oval; ventral apotome long, rectangular, completely separating genae ventrally; subocular ecdysial line absent; head setal pattern as in Fig. 2A, typical for family; mandibles short and wide, with short rounded teeth surrounding central concavity (Fig. 1D). Thorax (Figs. 1A, 1B); pronotum lacking anterolateral ecdysial lines, anterolateral corners with many setae; mesonotum covered by pair of large sclerites; each with single seta at *sa*1 position, 3 setae at *sa*2 position, and many setae at *sa*3 position; metanotum with large *sa*1 sclerites, each bearing single, long, anteromesal seta; small *sa*2 sclerites, each bearing 2 setae, one long, one very short; *sa*3 sclerites each bearing about 13 long setae; metasternum with broad, transverse patch of approximately 70 setae. Head and thoracic sclerites yellowish-brown, with many dark brown maculations as indicated in Fig. 1B. Legs long, slender, each bearing numerous long setae; yellowish brown in color; each leg segment with darkly pigmented, subterminal band (Fig. 1A). Abdomen (Fig. 1A): lateral hump sclerite of abdominal segment I as in Fig. 1A insert; lateral fringe present on segments III–VII; lateral tubercles present on segment VIII; segments I–VIII each with 1 or 2 pairs of very short, lateral setae; abdominal gills single, distributed as in Fig. 1A; dorsal sclerite of segment IX with 3 pairs of setae: long lateral and mesal pair and very short pair situated between those pairs; lateral sclerite of anal proleg large, bearing about 20 secondary setae; anal claw with 3 small dorsal accessory hooks; wide band of minute spines bordering anal opening (Fig. 1E). Length of larva 10–13 mm.

*Larval case:* Composed largely of plant fragments, rough, very slightly curved and tapered; often with 1 or more twigs extending beyond posterior end (Fig. 1C). Length of case 20–30 mm (excluding trailing twigs).

*Pupa:* Head (Fig. 2C): 2 pairs of long frontal setae; 1 pair of setae on vertex; 2 setae on each antennal scape; 2 setae below each eye; labrum with 6 pairs of long setae; mandibles long and slender, with fine serrations along inner margins; 2 setae on the lateral base of each mandible. Abdomen: gills, setation, and hook plates as in Fig. 2B; segment IX with small, dorsolateral protuberances, each bearing about 5 long setae; anal processes each long and slender, apical portion curved outward and bearing 4 setae (Fig. 4B). Long trailing twigs of larval case generally trimmed off before pupation. Rock fragments incorporated into anteroventral end of pupal case; anterior and posterior ends closed off with silk and debris.

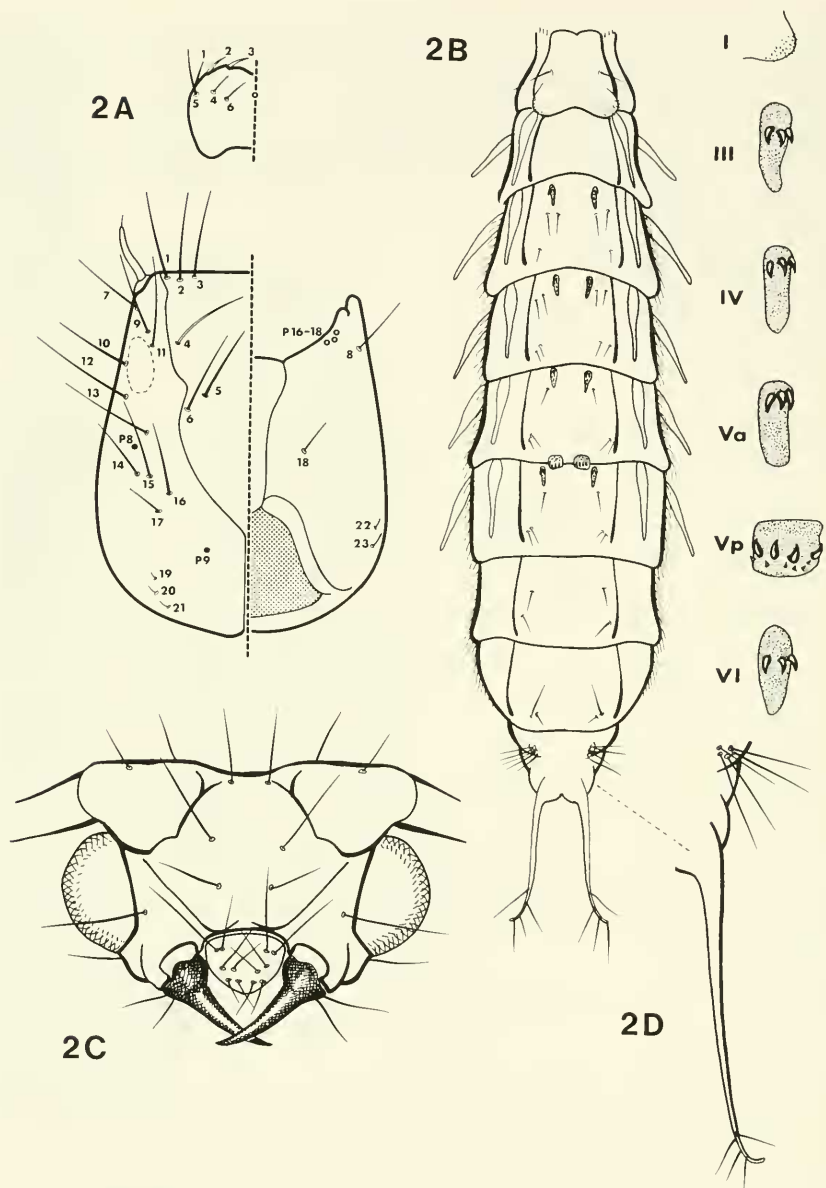Distribution.—Argentina: Chubut, Neuquén, Río Negro. Chile: Aconcagua, Ar-

Fig. 2. *Hudsonema flaminii* (Navás), larva and pupa. A, Larva, head and labrum (detached) setal pattern, left half dorsal, right half ventral. B, Pupa, abdomen, dorsal, hook plates enlarged. C, Pupa, head, frontal. D, Pupa, right anal process, dorsal.

auco, Atacama, Bío-Bío, Cautín, Chiloé, Concepción, Coquimbo, Curicó, Linares, Malleco, Maule, Ñuble, O'Higgins, Osorno, Santiago, Valdivia, Valparaíso.

Material examined.—Argentina: Chubut: Arroyo Golondrinas, 6 km N Lago Puelo, 8.ii.1974, O. S. Flint, Jr., many larvae; Lago Puelo, 8.ii.1974, O. S. Flint, Jr., many larvae; Río Epuyen, Hoyo de Epuyen, 10.ii.1974, O. S. Flint, Jr., one larva. Neuquén: 2 km SE Lago Lolog, 22.i.1974, O. S. Flint, Jr., many larvae; 5

km SE Lago Huechulafquen, 26.i.1974, O. S. Flint, Jr., many larvae, prepupae.
Río Negro: 5 km S Río Villegas, 7.ii.1974, O. S. Flint, Jr., female pupa, prepupae;
Cascada Mallin Ahogado, El Bolson, 9.ii.1974, O. S. Flint, Jr., many male, female
pupae. Chile: Malleco: Río Dumo, 11 km N Victoria, 300 m, 25.i.1978, C. M.
& O. S. Flint, Jr., many larvae.

## Key to Genera of Neotropical Triplectidinae (Adults)

1.  Hindwing fork III present in both sexes (i.e. M 3-branched); female
    forewing fork III present .............. Triplectidinae .............. 2
–   Hindwing fork III absent in both sexes (i.e. M 2-branched); female fore-
    wing fork III absent (except in *Amphoropsyche,* where it is present) ...
    .......................................................... Leptocerinae
2.  Forewing thyridial cell very long and slender, almost twice as long as
    discal cell ...................................................... 3
–   Forewing thyridial and discal cells subequal in length .............. 4
3.  Hindwing crossveins *rs* and *r-m* in line and fork I very narrow or absent;
    male inferior appendage without basoventral lobe or 2nd article ......
    ................................. *Notalina* (*Neonotalina*) Holzenthal
–   Hindwing crossvein *rs* apicad of *r-m* by at least its length and fork I,
    when present, not particularly narrow; male inferior appendage with ba-
    soventral lobe and 2nd article .................... *Triplectides* Kolenati
4.  Tibial spurs 2,2,4 ......................*Hudsonema flaminii* (Navás)
–   Tibial spurs 0,2,2 .............................................. 5
5.  Frontal setal wart long, narrow; 2nd article of male inferior appendage
    well developed, ½–1 × as long as apicodorsal portion of 1st article; male
    abdominal segment X without apical, digitate processes; female segment
    X without thin, ventrally directed, sclerotized plate below appendages of
    X ........................................... *Grumichella* Müller
–   Frontal setal wart oval; 2nd article of male inferior appendage under-
    developed, less than ¼ as long as apicodorsal portion of 1st article; male
    abdominal segment X with 2 pairs of apical, usually digitate, processes;
    female segment X with thin, ventrally directed, sclerotized plate below
    appendages of X ............................... *Atanatolica* Mosely

## Evolution

Ulmer (1906, 1907) first divided Leptoceridae into its two subfamilies Tri-
plectidinae and Leptocerinae based on whether the discal cell of the hindwing is
closed or open, respectively. Morse (1981) inferred monophyly for Triplectidinae
by the synapomorphic absence of the primitive phallic parameres and vestigial
phalicata ("aedeagus" of Nielsen, 1957); evidence for monophyly for Leptocerinae
was indicated by the absences of one branch of the median vein ("Fork 3") and
of the sectoral vein ("open discal cell") in the hindwing and the lack of preapical
spurs on the mesothoracic tibiae.

Morse (1981) further identified three tribes of Triplectidinae: Grumichellini,
Hudsonemini, and Triplectidini. Monophyly for Grumichellini was supported by
absences of apical spurs on the prothoracic tibiae and preapical spurs on the meso-
and metathoracic tibiae; for Hudsonemini, by the broad vertical plates of the
phallotremal sclerite; and for Triplectidini, by the possession of an extra appendage
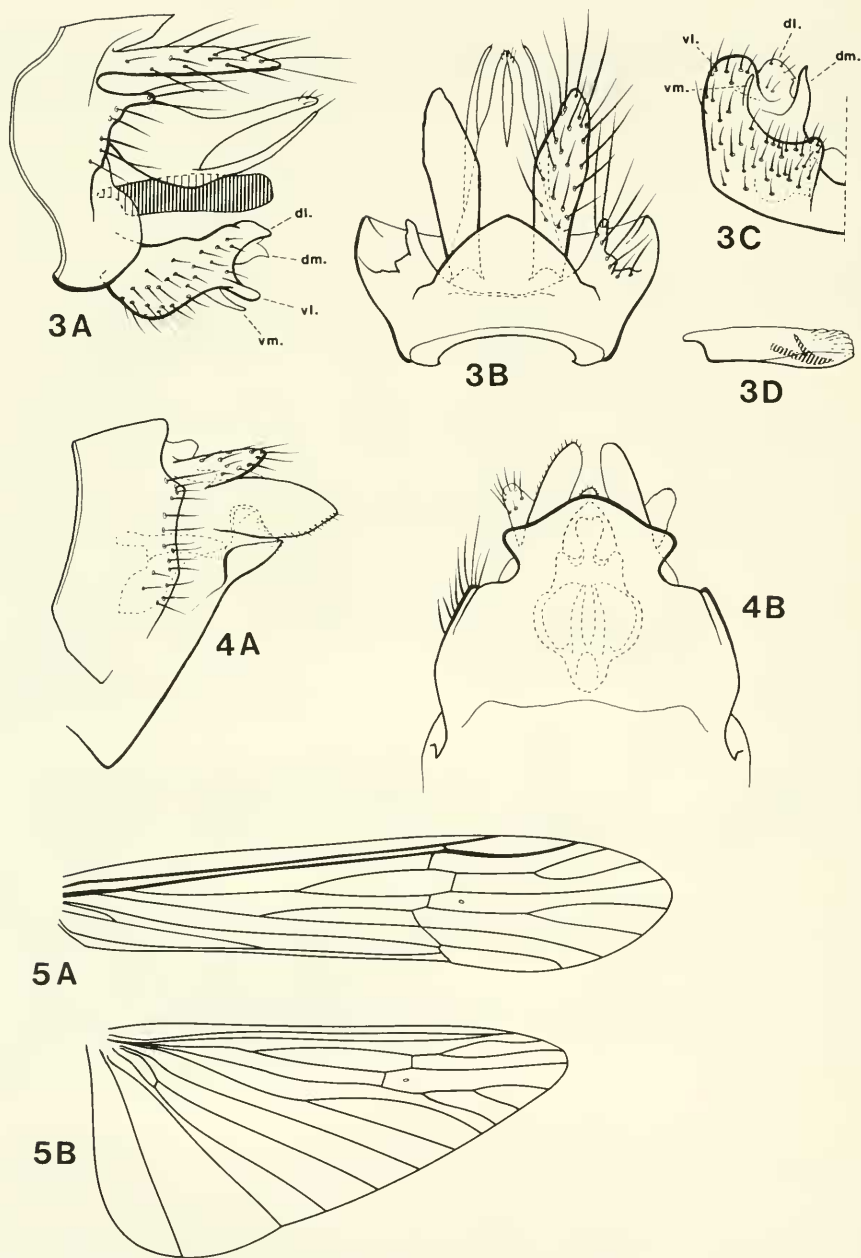
Figs. 3–5. *Hudsonema flaminii* (Navás). 3, Male genitalia. A, Lateral. B, Dorsal. C, Left inferior appendage, ventral. D, Phallic apparatus, lateral. 4, Female genitalia. A, Lateral. B, Ventral. 5, Male wings. A, Forewing. B, Hindwing.

articulating with the base of each inferior appendage. The historical relationships of the three tribes among themselves were left unresolved.

Morse (1981) placed *Hudsonema, Condocerus, Notalina,* and *Triplexa* in the Hudsonemini. However, *Triplexa* shares several unique genitalic and venational characters with the grumichelline genera *Atanatolica* and *Grumichella* (Holzen-

thal, unpublished) and is here removed from Hudsonemini and transferred to Grumichellini. Discovery of the immature stages of *Triplexa* possibly will test this phylogenetic hypothesis since known Grumichellini immature stages are highly derived, with several striking homologues.

Monophyly for the Hudsonemini is therefore supported by the following homologues (Fig. 6): (1) phallotermal sclerite with vertical extensions (Morse, 1981, fig. 2; Fig. 3D), (2) presence of secondary setae on lateral sclerite of each anal proleg (Fig. 1E; *cf.* Williams and Wiggins, 1981), and (3) absence (or fusion of vestige) of the 2nd article of each inferior appendage. The ventromesal spine on each inferior appendage of *Notalina* species (Holzenthal, 1986) and the ventromesal or dorsomesal spine on each inferior appendage of *H. flaminii* (Figs. 3A, 3C) may be the fused vestige of this 2nd article.

Within the Hudsonemini, the homologue which provides evidence for the monophyly of *Notalina* is (Fig. 6): (4) fork I of the hindwing very narrow, with a tendency to become lost. *Condocerus* and *Hudsonema* appear to be sister lineages because of: (5) shared possession of short, compact inferior appendages. Monophyly for the two species of *Condocerus* is supported by the following inferred homologues in the male genitalia: (6) abdominal segment IX "L"-shaped, broadest ventrally at point of insertion of inferior appendages; (7) inflected, spinose apices and (8) short, broad, triangular mesal lobes of the inferior appendages (Neboiss, 1977, figs. 747, 752).

There is no clear evidence for the monophyly of the three species of *Hudsonema*. Homologues are not evident in adult genitalia because of the obscuring effects of striking autapomorphies in *H. flaminii*. The pattern of setae and setal-bearing sclerites on the larvae of each of the three species is identical (Figs. 1A, 1B, 1E, 2A; Cowley, 1978, figs. 45, 46), except that in the New Zealand species metanotal *sa2* sclerites are absent. For example, larvae of all three species have a transverse row of numerous secondary setae on their metasterna; all have very similar lateral hump sclerites on abdominal segment I; and all have virtually identical terminal abdominal sclerites. Unfortunately, larval chaetotaxy of the Leptoceridae and related families has not been investigated to determine which conditions of setae and sclerites are part of their groundplan and which are derived from it. Thus, although together these phenetic characters distinguish *Hudsonema* larvae from related genera, they are not understood adequately to support monophyly. Taking the conservative taxonomic approach, therefore, *H. flaminii* is left as a species of *Hudsonema,* rather than transferred to *Condocerus* or to a new monotypic genus, on the supposition that: (9) one or more of the above phenotypic larval similarities will eventually be corroborated as homologous.

*Hudsonema aliena* and *H. amabilis* are considered to be sister species based on (Fig. 6): (10) very short, broad preanal appendages and (11) long, slender apicolateral extensions of the phallobase in the male genitalia (Mosely and Kimmins, 1953, figs. 165, 167).

## HISTORICAL BIOGEOGRAPHY

Triplectidinae are restricted to Australasia and the Neotropics; the subfamily Leptocerinae is cosmopolitan. Morse (1981) hypothesized that the Triplectidinae arose via vicariance as the South American-Antarctic-Australian landmass rifted from the rest of Gondwanaland 130–85 myBP.

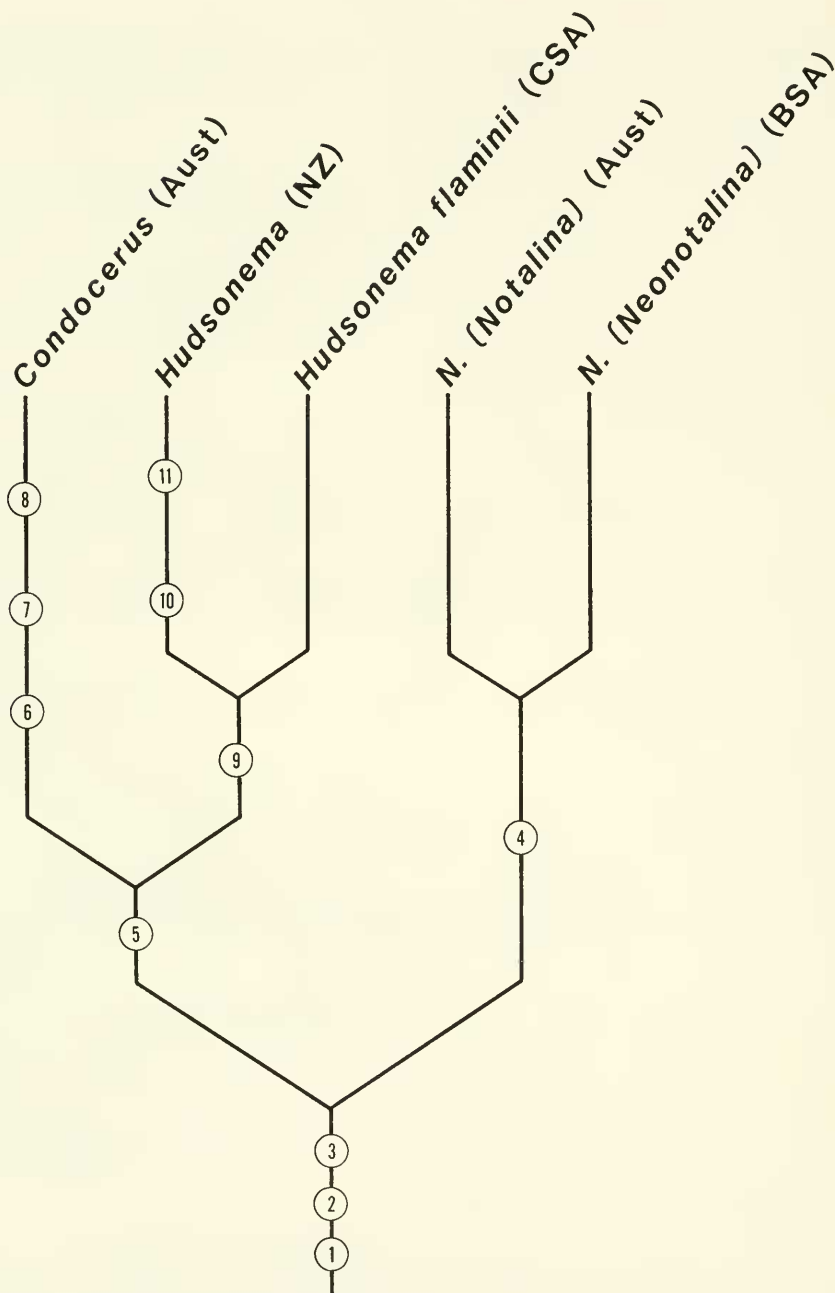Craw (1979, 1982) presented evidence indicating that the well-documented

Fig. 6.   Phylogeny of the genera of Hudsonemini.

trans-Antarctic distribution pattern is composed of two distinct biogeographical tracks: an Australian-South American track and a New Zealand-South American track. Many New Zealand and Chilean South American taxa are more closely related to each other than to Australian sister taxa. Caddisflies exhibiting this pattern include, in the Helicophidae, *Alloecentrella* (New Zealand) and *Alloecen-*
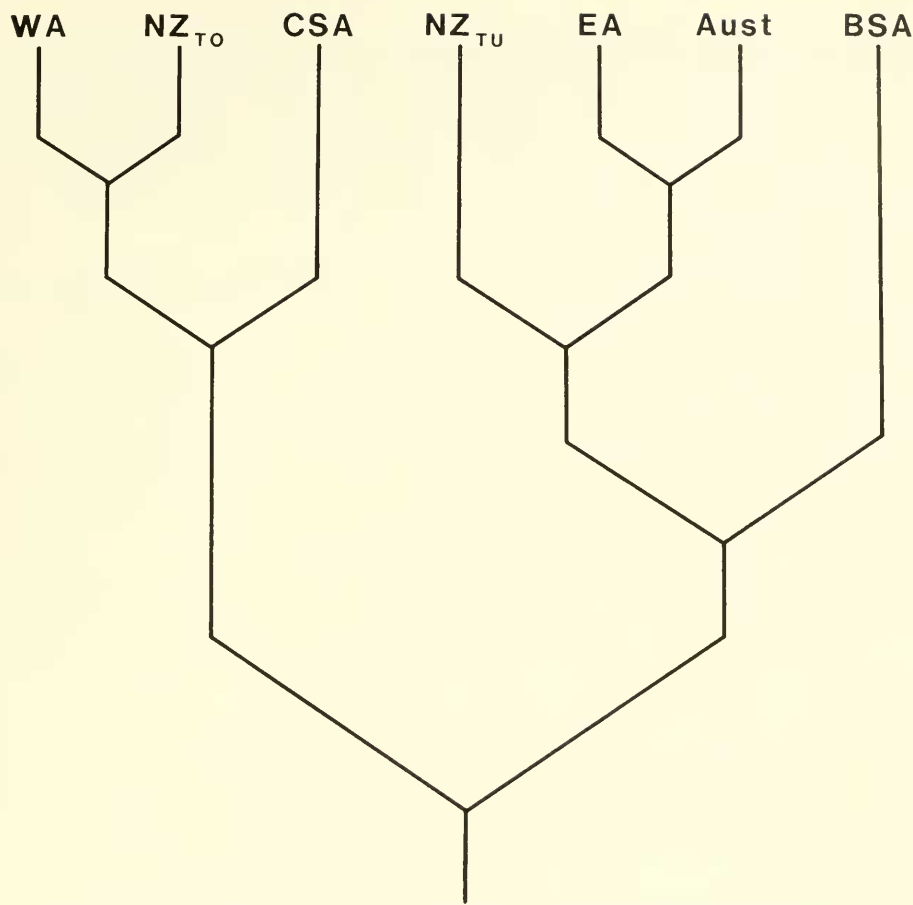
Fig. 7   Breakup of a section of Gondwanaland (adopted from Craw 1979, 1982, 1983).

*trellodes* (Chile) (Flint, 1979) and, in the Kokiriidae, *Kokiria* (New Zealand) and *Rhynchopsyche* (Chile) (Cowley, 1978). As indicated by the phylogeny discussed above, *Hudsonema* has two species in New Zealand (widely distributed and sympatric on both North and South Islands) and one species in Chilean South America. Its sister genus *Condocerus,* with two described species, is distributed in southwestern Western Australia, Victoria, and Tasmania.

Craw (1982, 1983; see also Platnick and Nelson, 1984) constructed a model of Pacific biogeography (Fig. 7) in which his Torlese terrane New Zealand ($NZ_{TO}$) was associated with Western Antarctica (WA) and Chilean South America (CSA). His Tuhua terrane New Zealand ($NZ_{TU}$) was associated with the eastern margin of the Australian plate (Aust) and East Antarctica (EA). This latter landmass had connections with Brazilian South America (BSA). $NZ_{TO}$-WA-CSA apparently separated from $NZ_{TU}$-EA-Aust-BSA during mid-Cretaceous times. This possibly resulted in the vicariant origins of *Hudsonema* and *Condocerus* populations on the former and latter landmasses, respectively, from a triplectidine ancestor primitively distributed over both. The model predicts that *Condocerus* species should occur in BSA and $NZ_{TU}$. The fact that such species are not known from these

regions may be due to extinction, but more likely, at least for BSA, is the result of an inadequately inventoried fauna; species of *Notalina* (*Neonotalina*), for instance, were recorded and described from the BSA Neotropics only very recently (Holzenthal, 1986). Subsequent separation of CSA from $NZ_{TO}$-WA and the former micro-continent's migration to its present association with BSA resulted in the present day disjunction seen in the distribution of *Hudsonema.* Sympatry of two of the *Hudsonema* species throughout New Zealand today is probably the result of recent dispersals.

Triplectidines exhibiting an Australian-South American trans-Antarctic track were possibly represented by an ancestral biota distributed over $NZ_{TU}$-EA-Aust-BSA that vicariated when BSA separated from $NZ_{TU}$-EA-Aust. Caddisfly relationships and distributions conforming to the latter scenario include species in *Notalina* and Grumichellini (here including *Triplexa*). Interestingly, Neotropical *Notalina* (*Neonotalina*) and the two Neotropical grumichellines, *Atanatolica* and *Grumichella,* are only known to occur today in BSA. These taxa may be descendants of a distinct, tropical component of the trans-Antarctic biota, traditionally accepted to have been temperate in nature (Cracraft, 1975). *Triplectides* species, although not yet analyzed phylogenetically, may conform to both Australian-South American and New Zealand-South American trans-Antarctic tracks; the genus has species in both BSA and CSA as well as Australia and New Zealand.

The phylogeny of the genera of Hudsonemini and, especially, the species of *Hudsonema,* presented above, is based upon few apparent homologues. That phylogeny (and the biogeographic interpretations based upon it), like all scientific hypotheses, is subject to further corroboration or falsification. Properly formulated, though, phylogenetic and vicariance hypotheses can be used to predict geographic and evolutionary patterns for as yet undiscovered or unstudied taxa (Morse and White, 1979; Savage, 1982). The geographic and evolutionary relationships of southern long-horned caddisflies support the predictions of Craw's model of Pacific biogeography as well as his contention that the trans-Antarctic distribution is a composite of at least two distinct biogeographical tracks.

ACKNOWLEDGMENTS

LITERATURE CITED

Cracraft, J. 1975. Historical biogeography and earth history: Perspectives for a future synthesis. Ann. Mo. Bot. Gard. 62: 227–250.

Craw, R. C. 1979. Generalized tracks and dispersal in biogeography: A response to R. M. McDowell. Syst. Zool. 28: 99–107.

———. 1982. Phylogenetics, areas, geology and the biogeography of Croizat: A radical view. Syst. Zool. 31: 304–316.

———. 1983. Panbiogeography and vicariance cladistics: Are they truly different? Syst. Zool. 32: 431–438.

Flint, O. S., Jr. 1967. Trichoptera collected by Prof. J. Illies in the Chilean subregion. Beitr. Neotrop. Fauna 5: 45–68.

———. 1974. Checklist of the Trichoptera, or caddisflies, of Chile. Rev. Chilena Entomol. 8: 83–93.

———. 1979. Studies of Neotropical caddisflies XXIII: New genera from the Chilean region. Proc. Biol. Soc. Wash. 92: 640–649.

Holzenthal, R. W. 1986. The Neotropical species of *Notalina,* a southern group of long-horned caddisflies (Trichoptera: Leptoceridae). Syst. Entomol. 11: 61–73.

Morse, J. C. 1975. A phylogeny and revision of the caddisfly genus *Ceraclea* (Trichoptera, Leptoceridae). Contrib. Am. Entomol. Inst. 11: 1–97.

———. 1981. A phylogeny and classification of the family group taxa of Leptoceridae (Trichoptera), pp. 257–264. Proc. 3rd Internatn. Symp. Trichoptera, ed. G. P. Moretti. Dr. W. Junk, Pub., The Hague. 486 pp.

Morse, J. C. and D. F. White, Jr. 1979. A technique of analysis of historical biogeography and other characters in comparative biology. Syst. Zool. 28: 356–365.

Mosely, M. E. 1936. A revision of the Triplectidinae, a subfamily of the Leptoceridae (Trichoptera). Trans. Roy. Entomol. Soc. Lond. 85: 91–129.

Mosely, M. E. and D. E. Kimmins. 1953. *The Trichoptera (Caddis-Flies) of Australia and New Zealand.* British Museum (Natural History), London. 550 pp.

Navás, L. 1926. Insectos neotropicos, 2a serie. Rev. Chilena Hist. Nat. 30: 326–336.

———. 1929. Insectos neotropicos (5a serie). Rev. Chilena Hist. Nat. 33: 17–24.

———. 1930. Algunos insectos de Chile, Serie 4a (1). Rev. Chilena Hist. Nat. 34: 350–366.

———. 1932a. Insectos de la Argentina y Chile, 3a Serie (1). Rev. Soc. Entomol. Argent. 5: 79–86.

———. 1932b. Décades de insectos nuevos. Década 20. Broteria Ser. Ciên. Nat. 1: 62–85.

———. 1933. Algunos insectos de Chile, 4a Serie. Rev. Chilena Hist. Nat. 37: 230–234.

Nielson, A. 1957. A comparative study of the genital segments and their appendages in male Trichoptera. Biol. Skr. Kong. Danske Vid. Selsk. 8: 1–159.

Neboiss, A. 1977. A taxonomic and zoogeographic study of Tasmanian caddis-flies (Insecta: Trichoptera). Mem. Nat. Mus. Victoria. 38: 1–208.

Platnick, N. I. and G. Nelson. 1984. Composite areas in vicariance biogeography. Syst. Zool. 33: 328–335.

Savage, J. M. 1982. The enigma of the Central American herpetofauna: Dispersals or vicariance. Ann. Mo. Bot. Gard. 69: 464–547.

Schmid, F. 1950. Les Trichoptères de la collection Navás. Eos 25: 305–426.

———. 1980. Les Insectes et Arachnides de Canada, Partie 7: Genera des Trichoptères du Canada et des États adjacent. Agriculture Canada. Ottawa. 296 pp.

Ulmer, G. 1906. Neuer Beitrag zur Kenntnis aussereuropäischer Trichopteren. Notes Leyden Mus. 28: 1–112.

———. 1907. Trichoptera. *In.* P. Wytsman, Genera Insectorum 60a: 1–259, 41 pls.

Wiggins, G. B. 1977. Larvae of the North American caddisfly (Trichoptera) genera. Univ. Toronto Press, Toronto. 401 pp.

———. 1984. Trichoptera, Chapter 16 (pp. 271–311). An introduction to the aquatic insects of North America, 2nd ed. eds. R. W. Merritt and K. W. Cummins. Kendall/Hunt, Dubuque. 722 pp.

Williams, N. E. and G. B. Wiggins. 1981. A proposed setal nomenclature and homology for larval Trichoptera, pp. 421–429. Proc. 3rd Internatn. Symp. Trichoptera. ed. G. P. Moretti. Dr. W. Junk, Pub., The Hague. 486 pp.